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MENDELIAN FACTOR DIFFERENCES VERSUS REACTION SYSTEM CONTRASTS IN HEREDITY. II

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The literature on species crosses shows clearly that all gradations occur as regards fertility from complete sterility to what is apparently complete fertility. Recombinations may, therefore, in some cases, occur freely between species that appear to be distinct. Lotsy (1913) in particular has shown this to be true for a number of species crosses in *Antirrhinum* and doubtless such instances might be multiplied considerably. But even in these cases the behavior of the hybrid progeny in subsequent generations indicates that there is a possibility that some of the recombinations do not form functional reaction systems because of the discordant elements they possess. This is shown in the entirely new characteristics which a certain portion of the population may exhibit and in the peculiar ratios which are sometimes obtained in segregation. Such results only bear out more completely the conception that for any recombination of elements to be completely functional they must together form a harmonious reaction system. Even Detlefsen's (1915) results with the cavy species cross which gave in F_1 sterile males and fertile females may be brought into line with such a physiological conception perhaps better than by trying to account for it on the basis of any definite number of Mendelian factors. At least in the cavy cross the attempt to account for the results in this latter manner demonstrated that the number of factors concerned must be relatively large, and this is precisely what would be expected on the basis of recombinations involving whole choromosomes or sections of chromosomes carrying with them, perhaps, many discordant elements. If we recall the observation that no crossing-over occurs in the sex heterozygote (Morgan et al, *l. c.*), presumably the male in this case, then it would be possible in the male cavy to secure only recombinations involving whole chromosomes, or in other words involving the building up of reaction systems with a large number of interchanged factors. In the female, however, these recombinations might include, in addition to those resulting from redistribution of whole chromosomes, cross-over gametes resulting from the exchange of sections of chromosomes. Such gametes might conceivably contain fewer discordant elements or they might be distributed in such a way as to distrub the reaction system thus formed less profoundly. Such data of course need first to be reexamined from this viewpoint before any definite conclusions can be reached, but the list of species hybrids which Detlefsen gives which result in sterile males and fertile females would seem to indicate that this is a phenomenon connected in some way with the observed lack of crossing-over in the sex-heterozygote already demonstrated in the work with *Drosophila* and the silkworm (Sturtevant, 1915). Until we know more about the fundamental basis of crossing-over and the factors affecting it, it is idle to speculate on such differences in behavior as are shown by males and females in the species crosses mentioned.

The insistent way in which the species hybrids between *Tabacum* and *sylvestris* point to the conception of the Mendelian reaction systems as units in themselves is of interest because of the broad and far reaching consequences which follow the application of such an idea. For if the nature of the progeny of these partially sterile hybrids as grown through several generations points to anything, it is that the abortive ovules and pollen grains represent a selective elimination of certain types of recombinations. Obviously, then, the presence of any considerable proportion of sterile ovules or pollen grains in plant material may be a consequence of hybridity and that of a rather profound type involving reaction systems which are more or less specific in their nature and in part incompatible with each other. The importance of this fact has, perhaps, not been sufficiently emphasized in work involving material which displays such partial sterility. Obviously, however, it is impossible to regard ratios obtained from such material as of any significance, unless it be possible to demonstrate definitely the nature of such gametes as fail to function. It is, therefore, not strange that species hybrids as a class require a somewhat different sort of treatment from that applicable to intervarietal crosses involving relatively few factor differences.

In the extensive work which has been done with the various species and forms of *Œnothera* this influence of partial sterility has undoubtedly played an important part, but at the same time one which has not been clearly defined. Jeffrey (1914) in particular has sought to establish the hybrid nature of *O. Lamarckiana* on the basis of the high percentage of abortive pollen grains which are found quite generally in the genus, and Heribert-Nilsson (1912) has attempted to analyze the material from a Mendelian standpoint. These attempts have not, however, led to a consistent explanation of the results observed, although they have established certain peculiar conditions in *Œnothera* which practically preclude the application of a rigid Mendelian analysis to such a type of behavior. On the other hand, a critical examination of the phenomena displayed by the various forms of *Œnothera* clearly indicates that these belong to several distinct categories, and not to one as is very generally assumed in discussions bearing on this subject. In this brief discussion we propose to classify them roughly as follows:

1. Strict factor mutations arising from unknown causes but clearly referable to specific germinal changes in isolated loci in the hereditary system. These display a simple, consistent Mendelian behavior when tested with the forms from which they arise. They usually show relatively simple and definite character differences when compared with the parent forms rather than complex differences throughout.

2. Segregation phenomena of a complex type resulting

in the constant and continual production of a number of distinct forms which display for the most part a complicated behavior when tested with the parents from which they arise and with other forms. Such forms are often widely different from the parent forms in all or nearly all of their characters.

3. Chromosome duplications resulting in duplication of one or more or even all of the chromosomes to the extent of tetraploidy in some forms.

The first of these categories may be rigidly distinguished from the other two, both of which may be fundamentally expressions of some inherent condition in the "mutating" individual. The existence of this first type of mutation can scarcely be denied in the face of the extensive evidence accumulated both on the plant and on the animal side. In addition to this long series of past observations, we have now the extensive work of Morgan and his associates (*l. c.*) in which the origin of over a hundred such factor mutations has occurred under observation in *Drosophila* cultures. These investigations indicate clearly that such mutations are fundamentally dependent upon actual changes in the germinal substance. They are the loss-mutations of genetic literature, but with the abandonment of the presence and absence hypothesis such a classification, of course, loses its significance. Practically always only one locus is involved in such a change, and the new form displays a consistent alternative behavior when tested with the form from which it arose. Such mutations are usually recessive, although a few dominant ones have been secured. When obtained in pure culture they show no tendency to revert to the parent form, at least not more frequently than they tend to change in entirely different directions. They are relatively rare, they do not recur in any definite considerable ratio in any strain, and they are not clearly due to any specific cause. In *Œnothera, rubricalyx* appears clearly to be a dominant mutation of this type (Gates, 1914). There seems to be little occasion for confusing these strict factor mutations with the more complex type of behavior included under the second and third categories.

When the second category is considered we are met with the task of harmonizing a large mass of rather confusing data, and it is perhaps true that this can not be done successfully at the present stage of our knowledge. There are not lacking, however, as many others have pointed out, a number of significant facts which are at least as logically explainable on the basis of hybridity as on assumptions of general germinal changes. If the results which have followed species crosses are to be extended to the type of behavior displayed by *Lamarckiana,* then it is clear that the numerical ratio in which segregation occurs is of no particular significance except in so far as its constancy indicates that it is due to a specific behavior in gametogenesis. Lotsy (1912) in particular has pointed out that in *Antirrhinum* species crosses, races may be secured which behave very much like some forms of *Œnothera* with respect to the segregation ratios obtained. The significant facts with which we have to deal are apparently, first that in *Œnothera* these "mutations" affect the sum total of the characters of the individuals, *i. e.,* they are dependent on complex germinal *differences* when compared with the parents, and second that these "mutations" continually recur within certain races in fairly constant ratios. These are facts which are just as simply explained on the basis of a complex type of segregation in which many of the systems formed contain discordant elements and therefore fail to develop as to refer them to actual change in germinal substance. Moreover, the former explanation harmonizes the results obtained with the simpler category of strictly Mendelian phenomena.

That this view of the *Œnothera* situation has something in its favor beyond the known general occurrence of partial sterility in this genus is shown by some of the results of hybridization between the various forms of *Œnothera.* The frequent appearance of F_1 populations consisting of distinct forms is usually taken to be an expression of segregation in the gametic series of such forms. Beyond this the *Œnothera* phenomena display a remarkably orderly behavior, and, although complex in nature, such orderliness points strongly to some kind of definite segregation dependent upon the hereditary constitution of the forms involved rather than upon any change in germinal substance expressed in the gametic series. *Lamarckiana*, for instance, produces constantly a small percentage of *nanella* as well as a number of other forms. It is, therefore, necessary to assume merely that *nanella* gametes make up a small percentage of the gametic series in *Lamarckiana*. When two *nanella* gametes meet, a *nanella* individual is produced, and it breeds true, as might be expected. When, however, a *nanella* gamete meets a *Lamarckiana* gamete a *Lamarckiana* individual is produced, which need not necessarily differ in its behavior with respect to the production of *nanella* from other *Lamarckiana* races, since practically all of the combinations involving *nanella* elements would fail to develop, or in case some few of these combinations did develop, they might produce other characteristic forms unlike either *Lamarckiana* or *nanella*. This conception is in part borne out by the fact that *nanella* appears to differ from *Lamarckiana* not only in stature, but also in other characters, as is shown in hybridization phenomena involving this form. From this standpoint also, the occurrence of *nanella* in the progeny of a wide range of forms is perfectly intelligible. When *nanella*, which apparently really breeds true, is crossed back with *Lamarckiana* a small proportion of the progeny is of the *nanella* type and the rest are *Lamarckiana*. This proportion is apparently greater than that normally obtained from selfed *Lamarckiana*, and this is merely a consequence of the realization of the gametic ratio of *nanellas* in the *Lamarckiana* series as a phenotypic ratio. The true breeding of the forms thus resulting, to the extent that they breed true, is a natural consequence of the germinal constitution of such forms. On the other hand, when *rubrinervis*, which never produces *nanella* as a "mutant" (Gates, 1915), is crossed with *nanella, nanella* does not appear in F_1, and in F_2 appears in a fairly definite ratio in the progeny of the *subrobusta* forms thus produced (de Vries, 1913), whereas the *Lamarckiana* forms produced breed true, after their usual fashion. Obviously this behavior is simply a consequence of the fact that *rubrinervis* does not produce a gametic series containing *nanella,* and, therefore, *nanella* can not appear in F_1. The impressively orderly behavior throughout in these hybridization phenomena is an eloquent testimony of the existence of a casual agency of a simpler nature than that called for under the hypothesis of actual, germinal changes.

Those phenomena included in the third category and dealing with chromosome duplication may be referred to the same type of iregular behavior in gametogenesis as is concerned in the production of the other "mutants." They are of interest most particularly from our standpoint with regard to the structural relations which they display in comparison with the other forms. Thus there is a series of *lata* forms dependent on the duplication of one chromosome in *Lamarckiana.* They are not identical within the series, but at least three or four are known which differ from one another in a characteristic fashion. This may well be dependent on the particular chromosome pair which is concerned in the duplication as Gates (1908) has suggested. According to the chromosome view of heredity this duplication has the effect of altering the proportions of the various elements in the reaction system, and naturally in a delicately balanced system such alteration results in a change in the somatogenic processes in a definite direction, the latter dependent upon which particular elements are increased. Since a whole chromosome with presumably a large set of factors is involved, it should follow that the entire set of characters of the plant would be affected, as appears actually to be the case. The important point in connection with these phenomena is the apparent consequence that phenotypic changes may be dependent merely on an alteration in the relative quantitative proportions of the

Mendelian units making up the reaction systems. Apparently this will account satisfactorily for the orderly resemblance of these chromosome "mutants" to each other and to the forms from which they arise. Conceivably the great body of data on which the mutation theory is based would, for the most part, find a simpler explanation along the lines thus indicated.

SUMMARY

Summarizing briefly the content of this paper, the following facts have, on the experimental side, been presented with reference to a species hybrid:

1. *N. sylvestris* when crossed with various varieties of *N. Tabacum* gives F_1 hybrids which are replicas on a large scale of the particular *Tabacum* variety concerned in the cross.
2. The F_1 hybrids of *sylvestris* and *Tabacum* produce a small number of functional ovules which represent the *sylvestris* and *Tabacum* extremes of a recombination series, the great majority of the members of which fail to function because of mutual incompatibility of the elements of the two systems.
3. Back crosses with *sylvestris* give *sylvestris* and aberrant forms, and of the two the *sylvestris* alone are fertile and breed true. On the other hand, back crosses with *Tabacum* produce apparently only *Tabacum* forms of which some are completely fertile and continue to produce only *Tabacum* forms.

On the theoretical side the following conclusions have been drawn and their application indicated:

1. As a consequence of modern Mendelian developments, the Mendelian factors may be considered as making up a reaction system the elements of which exhibit more or less specific relations to one another.
2. Strictly Mendelian results are to be expected only when the contrast is between factor differences within a common Mendelian reaction system as is ordinarily the case in varietal hybrids.

3. When distinct reaction systems are involved, as in species crosses, the phenomena must be viewed in the light of a contrast between systems rather than between specific factor differences, and the results obtained will depend upon the degree of mutual compatibility displayed between the specific elements of the two systems.

4. Sterility in such cases depends upon non-specific incompatibility displayed between the elements of the systems involved, and the degree of this sterility depends upon the degree of such incompatibility rather than upon a certain number of factors concerned in the expression of such behavior.

5. The consequences of the application of such a conception to the complex type of behavior in *Œnothera* are pointed out, and the suggestion is specifically made that the type of behavior exhibited by *Lamarckiana* and its segregants in hybridization may be referred to such complex system interactions.

LITERATURE CITED

Bateson, W., and Punnett, R. C.
1912. Experimental Studies in the Physiology of Heredity. *Proc. Roy. Soc. London, Rept. Evol. Com.*, IV: 6–18.

Conklin, E. G.
1908. The Mechanism of Heredity. *Science,* N. S., 27: 89–99.

Correns, C.
1913. Selbststerilität und Individualstoffe. *Biol. Centralb.* 33: 389–423.

Detlefsen, J. A.
1914. Genetic Studies on a Cavy Species Cross. *Publ. Carnegie Inst. Washington,* No. 205, pp. 1–134, 1914.

East, E. M.
1915. An Interpretation of Sterility in Certain Plants. *Proc. Amer. Phil. Soc.,* 53: 70–72.

East, E. M., and Hayes, H. K.
1912. Heterozygosis in Evolution and in Plant Breeding. *U. S. Dept. Agr. Bur. Pl. Ind.,* Bul. No. 243: 1–58.

Gates, R. R.
1908. A Study of Reduction in *Œnothera rubrinervis. Bot. Gazette,* 45: 1–34.
1914. Breeding Experiments which Show that Hybridization and Mutation are Independent Phenomena. *Z. Abst. Vererbl.,* 11: 209–279.
1915. The Mutation Factor in Evolution.

Goodspeed, T. H.

1913. On the Partial Sterility of *Nicotiana* Hybrids Made with *N. sylvestris* as a Parent. *Univ. Calif. Publ. Botany,* 5: 189–198.

1915. Parthenogenesis, Parthenocarpy, and Phenospermy in *Nicotiana. Univ. Calif. Publ. Botany,* 5: 249–272.

Goodspeed, T. H., and Ayres, A. H.

1916. On the Partial Sterility of *Nicotiana* Hybrids Made with *N. sylvestris* as a Parent. II. *Univ. Calif. Publ. Botany,* 5: in press.

Heribert-Nilsson, N.

1912. Die Variabilität der *Œnothera Lamarckiana* und das Problem der Mutation. *Z. Abst. Vererbl.,* 8: 89–231.

Jeffrey, E. C.

1914. Spore Conditions in Hybrids and the Mutation Hypothesis of de Vries. *Bot. Gazette,* 58: 322–336.

Jennings, H. S.

1914. Development and Inheritance—Its Relation to the Germ. *The Johns Hopkins Univ. Circ.,* 1914, No. 10.

Lotsy, J. P.

1912. Versuche über Artbastarde und Betrachtungen über die Möglichkeit einer Evolution trotz Artbeständigkeit. *Z. Abst. Vererbl.,* 8: 325–332.

1913. Hybrides entre espèces d'*Antirrhinum.* IV. *Conf. Inter. Genetique,* pp. 416–428.

Miles, F. C.

1915. A Genetic and Cytological Study of Certain Types of Albinism in Maize. *Jour. Genetics,* 4: 193–214.

Morgan, T. H.

1914. Two Sex-Linked Lethal Factors in *Drosophila* and Their Influence on the Sex Ratio. *Journ. Exper. Zoology,* 17: 81–122.

1915a. The Rôle of the Environment in the Realization of a Sex-Linked Mendelian Character in *Drosophila.* AMER. NAT., 49: 385–429, 1915.

1915b. The Constitution of the Hereditary Material. *Proc. Amer. Phil. Soc.,* 54: 143–153.

Morgan, T. H., Sturtevant, A. H., Muller, H. J., and Bridges, C. B.

1915. The Mechanism of Mendelian Heredity.

Pearl, R.

1915. Modes of Research in Genetics.

Setchell, W. A.

1912. Studies in *Nicotiana.* I. *Univ. Calif. Publ. Botany,* 5: 1–86.

Sturtevant, A. H.

1915. No Crossing-over in the Female of the Silkworm Moth. AMER. NAT., 49: 42–44.

de Vries, H.

1913. Gruppenweise Artbildung, p. 215.

Wilson, E. B.

1914. The Bearing of Cytological Research on Heredity. *Proc. Roy. Soc. London,* B88: 333–352.